THE EFFECT OF TEMPERATURE ON TESTICULAR RECRUDESCENCE IN JUNCOS AT DIFFERENT PHOTOPERIODS[1]

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Some, perhaps many, biologists specializing in field observations are unwilling to accept the concept, developed through three decades of experimental work, that length of the daily periods of light and darkness, and their seasonal changes, play a fundamental role in regulating the annual reproductive cycle in birds. Thus, Blanchard (1941, p. 76) deems it ". . . extremely doubtful whether the abundant means which have been discovered for upsetting the physiological balance of captive birds should be accepted as possessing any bearing whatever on the factors which control the cycle under natural conditions." She believes (p. 74) that temperature is the most important single factor lying at the ultimate source of annual variations of the gonad cycle in white-crowned sparrows. Marshall (1951, p. 245) calls for "far more elegant experimental techniques than those used in the past . . . before it can be unquestionably accepted that light fluctuation causes . . . prenuptial sexual recrudescence." He holds (p. 257) that the annual cycle is kept in step with the sun not by the changing photoperiod but by external factors that permit nest building and the events subsequent to nest building, and he includes "mild weather" among the probably most important of these external factors.

The literature dealing with experimental studies of the effect of temperature and day-length on the gonads of birds has been reviewed by Burger (1949). Two papers published prior to that time are especially pertinent to the present study. Burger (1948) found that when starlings are subjected to relatively constant high temperatures (either 32°–35° C. or 38°–40° C.) testicular recrudescence proceeds at a rate faster than when birds are exposed to fluctuating moderate temperatures (11°–24° C., with a daily range of about 6°), providing that the photoperiod is favorable. On the other hand, Kendeigh (1941) found that exposure to fluctuating outdoor temperatures averaging about 2° C. did *not* limit gonad increase under lengthened photoperiod in the English sparrow. More recently Farner and Mewaldt (1952), in a study on white-crowned sparrows of which we have seen only an abstract, conclude (p. 107) that "if photoperiod and light intensity are sufficient to induce early recrudescence, the rate of recrudescence can be accelerated by increased temperature."

The experiments now to be reported do not have the "elegant" design called for by Marshall, but they are the first to test the effect of moderately high and low temperatures on testicular recrudescence in birds exposed to different photoperiods near the supposedly critical or minimum limit. For an understanding of the relative importance of these two factors, temperature and day-length, in the timing of

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the early phases of seasonal reproduction it seems especially important to study their interaction at levels near those occurring in nature at the time these early gonad changes are taking place. The importance of approaching the subject in this way seems obvious, yet in the much-studied field of bird photoperiodism no such study has been made heretofore. The results, we hope, may promote reconciliation of some opposing views and apparently contradictory statements to be found in the literature.

Materials and Methods

Sixty-six male Juncos and two females were used in the experiments. Presumably of the race *Junco hyemalis hyemalis* (Miller, 1941; pp. 321, 329), all were trapped or netted in the immediate vicinity of Chapel Hill, N. C. The birds of groups G, H and J (Table I) were taken in late November and (mostly) in December, 1954; those of groups A through F were captured in January and February (A, B and C in 1954; D, E and F in 1955). Birds collected at any one time were assigned at random to the several groups by the turning of cards. (Scatter diagrams of the results indicate no correlation with date of capture.) Each group of birds was confined in a cage made of ¼ inch-mesh hardware cloth and measuring 36 in. × 24 in. × 24 in.; they were fed a commercial chick mash (Purina Growena). Until experimental lighting was begun (Table I, "Dates"), the birds were held in an unheated attic near a small, north-facing window, hence on nearly natural day-lengths. For the experiments, the cages were placed each in a light-tight, ventilated compartment measuring approximately 60 in. × 48 in. × 48 in., lighted by two 100-watt white-color fluorescent tubes. The lights were operated by automatic timer switches; they delivered approximately 150 foot-candles of light on the floor of the cage. A Taylor maximum-minimum thermometer was placed beside each cage and the temperatures recorded daily. Groups A through F were held on a 10-hour photoperiod until the middle of April; then, for six weeks they were exposed to the test photoperiod (10, 11 or 12 hours), certain of the groups being transferred for this test period to a cold-room maintained at 4°–8° C. Group C was placed in the cold-room during the dark period only, and removed daily to a relatively warm room for the lighted period. At the end of the test period the birds were sacrificed and the testes fixed *in situ* in Helley's fluid. Subsequently, after one week in 80% alcohol, the testes were measured, under a binocular dissecting microscope, with vernier calipers reading to 0.1 mm. From these measurements volumes were calculated according to the rule for a prolate spheroid. Later one testis of each bird was excised and eventually sectioned for determination of spermatogenic state and measurement of tubule diameter.

We chose photoperiods of 12 hours and less because we thought that a longer day-length might mask any temperature effect (as apparently it did in the experiments of Kendeigh, 1941). Also, day-lengths of less than 12 hours more nearly correspond to the natural day-lengths of winter, when birds normally are exposed to lower temperatures. Three different photoperiods were used to permit expression of the effect of length of day independently of the effect of temperature. We chose a test period of only six weeks again to prevent any masking of the effect of temperature—what was to be measured, essentially, was the rate of re-growth of the testes, and over a longer period of time birds exposed to the more adverse

experimental environment might have approached the plateau of the growth curve reached earlier by birds enjoying more favorable conditions.

Admittedly, it would have been immensely desirable to begin all test periods on or near the winter solstice, when natural day-length is shortest and when, presumably, the testes of any Junco taken in the field would be in an entirely inactive state. This was not done for the primary reason that we were unable to obtain birds in numbers sufficient to our purpose by that time. Bearing in mind, then, that by February, when some birds in each of the groups A through F were taken, spermatogenic activity had begun, with at least a considerable increase in the number of large Leydig interstitial cells, we held all birds of these groups for about eight weeks on a 10-hour photoperiod, expecting that on such a photoperiod and for such a time all birds would be reasonably "evened up." (We had the further consideration that by late spring the sun would have heated up the attic, where our light-tight compartments are installed, thus increasing the temperature contrast with the cold-room, but this now seems to have been an unnecessary precaution.) At any rate, groups G, H and especially J, which were put on test schedules on Dec. 21, provide some basis for comparison, and for judging the validity of our results.

We are indebted to our colleagues, Dr. Harry Smith and Mr. Edmund Gehan, of the Department of Biostatistics, for statistical analyses of testes volume.

Results

The day before the first three groups were started on a 12-hour photoperiod one bird of group A was found dead, and one also of group B, the deaths presumably due to injury occurring during transfer to clean cages. They provide some indication of the condition of the testes at this time, after about eight weeks on a 10-hour photoperiod (Feb. 16–Apr. 10). The combined volume of right and left testes of one was 2.5 mm.^{3}, the other 1.4 mm.^{3} Both were in stage III (Blanchard, 1941), not yet having reached the stage of division of spermatocytes.

12-hour photoperiod. Six weeks after the beginning of the test period on Apr. 11, the average paired testes volume in the birds of group A had increased approximately 50-fold, reaching 116.2 mm.^{3} (Table I). However, these birds, in warm cages, were far advanced in testicular development over the birds of group B, held in a relatively cold environment, the average volume of the paired testes in group A being approximately four times that of the testes in group B. They were similarly advanced over the birds of group C, which were warmed during the lighted portion of the day but exposed to the cold daily during the dark period. The differences in average volume are significant at the 0.1% level, both between A–B and A–C. The apparent difference between B and C is not statistically significant.

Fully formed spermatozoa were present in at least small numbers in each tubule of seven of the eight birds in group A, but only six of fifteen birds in groups B and C had reached that condition (Blanchard's late stage VI), thus 88% in A, only 40% in B and C. None of the testes from birds of groups B and C had tubules packed with sperm bundles, although four in group A had attained that stage (Blanchard's stage VII).

11-hour photoperiod. The difference between birds exposed to high and low temperatures when on an 11-hr. photoperiod (groups D and E, Table I) is less

marked, the difference in average testes volume being significant only between the 5%–10% levels. This low level of significance is largely due to the great variability shown by the birds of group D—in four of the nine, paired testes volume ranged from 18.2 mm^3 to 52.3 mm^3, while in another four it ranged from 2.9 mm^3 to 5.4 mm^3. In group E, however, the largest paired testes volume was 12.2 mm^3; in six of the eight birds it ranged from 3.0 mm^3 to 4.6 mm^3. Of these two groups on an 11-hr. photoperiod the testes of only one bird had developed spermatozoa (Blanchard's late stage VI), this being the most advanced bird in group D. The

TABLE I

Summary of experimental conditions and resultant data

Group	*n*	Dates	Daily temp. °C.		Photo-period hrs.	Mean vol. pr. testes mm^3	No. with sperm	Beyond stage III*
			Ave. max.	Ave. min.				
A	8	Feb. 16–Apr. 11	‡	‡	10			
		Apr. 11–May 24, '54	29.0	23.5	12	116.2	7	100%
B	7	Feb. 16–Apr. 11	‡	‡	10			
		Apr. 11–May 24, '54	8.6	4.0	12	26.3	2	100%
C	8	Feb. 16–Apr. 11	‡	‡	10			
		Apr. 11–May 24, '54	25.2	4.0	12	35.6	4	100%
D	9	Feb. 16–Apr. 9	26.3	20.6	10			
		Apr. 9–May 21, '55	29.9	24.9	11	16.9	1	100%
E	8	Feb. 16–Apr. 9	26.6	20.8	10			
		Apr. 9–May 21, '55	8.6	4.5	11	5.4	0	75%
F	7	Feb. 16–Apr. 9	26.8	20.6	10			
		Apr. 9–May 21, '55	29.3	24.5	10	5.2	0	30%
G	8	Dec. 21–Feb. 1, '55	26.3	19.5	11	1.4	0	0
H	7	Dec. 21–Feb. 1, '55	8.2	4.3	11	1.2	0	0
J	4	Dec. 21–Feb. 16	25.0	19.5	11			
	(+ 2 ♀ ♀)	Feb. 16–Apr. 9	25.9	20.6	11			
		Apr. 9–May 21, '55	28.9	24.5	11	14.9	1	100%

* Attainment of stage IV, beginning of spermatocyte division, coincides in white-crowned sparrows with the beginning of territorial activity in resident populations; in migratory populations it shortly precedes start of the spring migration (Blanchard, 1941).

‡ Temperatures were not recorded for groups A, B, and C during the period Feb. 16–Apr. 11, 1954; but these birds were in the same compartments as used for D, E and F in 1955 and temperatures were certainly in the general range 20°–25° C.

difference in average testes volume between B (12-hr., cold) and D (11-hr., warm) is not demonstrably significant; that between C (12-hr., warm day, cold night) and D is on the borderline of statistical significance.

When an 11-hr. photoperiod was similarly tested but beginning Dec. 21, advance in spermatogenesis was slight by the end of the test period on Feb. 1 (groups G and H, Table I). The testes of no one of these birds reached stage IV, the beginning of division of spermatocytes, although one in group G was very near to that point. Most were in stage III. The difference between G and H in testes volume

is not statistically significant, but it may be noted that it is the cold group H which shows the lowest average volume and that it is the warm group G in which the most advanced individual occurs. Measurements of maximum tubule diameter agree with calculation of testes volume—in the warm group G maximum tubule diameters averaged 75.8 μ, in the cold group H only 66.7 μ.

In another experiment (group J, Table I), four males were exposed to warm temperatures and to a day-length of 11 hours for five calendar months (Dec. 21–May 21). Two females were caged with them throughout this time, an arrangement which we expected would enhance the chances of the males developing larger testes, as has been demonstrated, on a longer day, for starlings (Burger, 1953). In only one Junco of this group, however, did the testes develop to a stage at which spermatozoa were present (45.8 mm^3, late stage VI). The next largest pair of testes had a volume of 6.9 mm^3 (stage V), the smallest only 2.3 mm^3 (early stage IV, *i.e.,* first appearance of spermatocyte division). The range of development was close to that in group D (largest 52.3 mm^3 in D, 45.8 mm^3 in J; 55% under 10.5 mm^3 in D, 75% under 7.0 mm^3 in J).

10-hour photoperiod. For practical reasons having to do with available space and available numbers of male Juncos, a 10-hr. photoperiod was not tested in the cold-room, but only in the warm temperatures of the attic (group F, Table I). None of the seven birds in this test developed spermatozoa, although the testes of one, by far the most advanced, reached a mature stage V, the tubules being packed with primary spermatocytes undergoing division (testes volume 22.6 mm^3). The testes of only one of the remainder showed any dividing spermatocytes (stage IV; testes volume 3.0 mm^3). Testes of five of the seven birds were still in stage III; in three of these, testes volume was less than 2.0 mm^3. The largest pair of testes exceeded the next largest by more than 500%. If this extreme high value is rejected from the statistical analysis, then the difference in the average volumes between group E (11-hr., cold) and group F (10-hr., warm) is significant at the 2%–5% level. That is, in most Juncos recrudescence of the testes proceeds at a measurably faster rate in the cold on an 11-hr. photoperiod than in warmth on a 10-hr. photoperiod.

Discussion

The above results seem clearly to demonstrate that if Juncos are subjected to low temperatures during the period of testicular recrudescence the rate of recrudescence will be retarded (or that, conversely, the rate will be accelerated in birds enjoying a warmer environment). This temperature effect is especially concise in groups A and B, as also in A and C; it is evident, too, in groups D and E. Comparison of groups B and C at least suggests that average daily temperature may be more important than minimum temperature, although the data are insufficient for a precise demonstration.

To this extent our experimental results confirm the conclusions drawn from field observations by Blanchard (1941) and by Marshall (1951) as to the effect of temperature on the annual recrudescence of the avian testis. But additionally they demonstrate, we believe, a decisive limitation on the favorable effects of warm temperature, the limiting factor being a favorable day-length, confirming then also the conclusions of Burger (1948). Two of seven of our birds on a 12-hr. photoperiod

in a continuously cold environment developed spermatozoa, as well as four of eight exposed to warm days and cold nights, but only one of nine in continuously warm surroundings on an 11-hr. photoperiod did so. Thus, rate of testicular recrudescence in Juncos under favorable temperature conditions on an 11-hr. photoperiod is certainly no faster, and is perhaps somewhat slower, than it is under poor conditions of temperature but with an additional hour of light (group D versus group B or C). In testes of six of eight birds kept in the cold-room on an 11-hr. photoperiod (group E) primary spermatocytes were undergoing division; on a 10-hr. photoperiod in a warm environment (group F) only two of seven attained this stage. In neither of these groups were spermatozoa developed. If we combine results on different day-lengths (groups A through F) we note that while thirteen of twenty-three birds on a 12-hr. photoperiod (56%) developed spermatozoa, only one of seventeen on an 11-hr. photoperiod (6%) and none of seven on a 10-hr. photoperiod (zero %) did so. Therefore, at these day-lengths and temperatures—both of which are reasonable when compared to conditions in nature—length of the photoperiod is shown clearly to be a more fundamental limiting factor in rate of testicular recrudescence than is temperature. Evidence that this conclusion is valid also for another passerine bird (*Zonotrichia leucophrys gambeli*) is apparent in the data of Farner and Mewaldt (1953), since their individuals kept at about 0° C. on a constant 15-hour day far exceeded, in testicular development, individuals kept in surroundings of 21° C. on natural day-lengths under 12 hours long. Kendeigh's (1941) conclusion that temperatures averaging 2° C. do *not* limit gonad development is not contradictory to our results with low temperatures; the seeming contradiction receives a logical interpretation in terms of day-length. That is, Kendeigh employed a long photoperiod (up to 15 hours), thus further augmenting the already stronger influence of length of day, and this augmentation overrode completely, or at least eventually, the retarding effect of low temperature.

If the validity of our results is questioned because of the several weeks through which we held birds on a 10-hr. photoperiod before beginning the test schedules, we may emphasize justifiably our experiment J, despite the small number of birds involved. These four male Juncos were placed on an 11-hr. photoperiod on the day of the winter solstice; although they were kept warm and had the company of two females, only one had developed spermatozoa even after five months. The testes of this one were next to the smallest of any of the fifteen which developed spermatozoa in these experiments and, judging from tubule size, were just out of the stage of predominance of spermatids. The next largest pair of testes in this group J was smaller than any but one of the twenty-three in our 12-hour groups. The range of development was entirely comparable to that in group D, which were on an 11-hr. photoperiod from Apr. 9 to May 21. All of this strongly suggests to us that on an 11-hr. photoperiod under otherwise favorable experimental conditions most Juncos cannot develop spermatozoa even after several months.

The relatively slight testicular development in those birds exposed to an 11-hr. photoperiod for six weeks beginning at the winter solstice (groups G, H) suggests that our later birds (groups A–F) were somehow conditioned to a more rapid, or greater, response as a result of their long experience of a 10-hr. photoperiod following natural day-lengths to Feb. 16. This is in agreement with the findings of Vaugien (1955) on young house sparrows (*Passer domesticus*). His data demon-

strate a progressive increase in testicular weights of sparrows exposed to continuous illumination for four weeks beginning at successive intervals from fall to spring. We would expect, then, if all experiments had been started on Dec. 21, a lesser degree of response in each group after six weeks of treatment. But since all the birds of our groups A to F had experienced essentially identical day-lengths prior to mid-April, the nature of the differences in results can be ascribed confidently to differences in the experimental environment during the ensuing six weeks.

We have not conclusively demonstrated the existence of a minimum or critical length of day, since at least some spermatogenic activity occurred even in our 10-hr. group. The possibility remains that on the shortest days there proceeds, albeit very slowly, at least the earliest stages of recrudescence, *i.e.*, development of functional interstitial cells and multiplication of spermatogonia. Our results suggest, however, that for Juncos days longer than 10 hours are necessary at least to pass beyond the first meiotic division, and it may well be that it is at this stage that length of day becomes the critical factor. An essentially similar conclusion is drawn by Miller (1955) with respect to golden-crowned sparrows (*Zonotrichia coronata*), from results of experiments in which birds were placed on a 10-hr. photoperiod beginning at the winter solstice and sampled at intervals during the following spring and summer. He interprets his data as demonstrating an innate tendency to recrudesce, more or less on schedule, but notes that, on a constant 10-hr. day, this innate process falls short of the level of completion of the maturation divisions, reaching a maximum of stage V with subsequent regression to a resting state.

Our experiments were not continued over as long a period as these of Miller. However, one of our Juncos on a 10-hr. photoperiod reached stage IV, and one which reached stage V approached the next stage, the appearance of spermatids. The relatively advanced state of the testes of this one bird may perhaps point to a further conclusion, when considered together with extreme cases in other groups. In each of five of the six groups A through F, one individual was considerably advanced over all others in its group; in the other group (C) two were so advanced. In group A, the largest pair of testes exceeded the next largest by 25%, in group B this value amounted to 60%, (in C to 10%), in D to 80%, in E to 54%, in F to 510% (and in J to 563%!). In group C the average of the two largest pairs of testes exceeds the third largest pair by 63%; the comparable value in A is 43.5%. That such variations are natural phenomena, and not bizarre experimental results, is evident in recorded field observations, for example, those of Blanchard (1941, p. 56 and Fig. 25) on white-crowned sparrows and of Kirschbaum and Ringoen (1936, Table I) on English sparrows. An explanation for these exceptional Juncos, which we believe to be an entirely plausible and reasonable one, lies in the prospect that individuals vary as to the threshold of response to external stimuli to testicular recrudescence, and that for a very few individuals this threshold is relatively low, occurring even perhaps on a 10-hr. photoperiod and manifesting itself at least under favorable temperature conditions after a long period of time.

Our experiments do not touch on the question as to the point in Junco physiology at which either day-length or temperature exerts its primary or immediate effect. As to temperature it has been suggested by Davis and Davis (1954) that increased thyroid activity induced by a cold environment interferes in some way

with testicular activity, possibly from an antagonism of the thyrotropic and gonadotropic functions of the pituitary. At any rate, our results with a 12-hr. photoperiod in cold surroundings show that low temperature alone is not a limiting factor, and such experiments as Kendeigh's indicate that on relatively long days the photoperiodic mechanism completely overrides the temperature mechanism. Also, there are many recorded cases of sperm development in males, and production of fertile eggs in females, in birds exposed to freezing temperatures on a long photoperiod (*cf.* Burger, 1949). We must conclude that day-length is in some way an integral part of the mechanism of testicular recrudescence, being either permissive or prohibitive of sperm development above or below approximately 11 hours in Juncos, and that temperature plays at best a modifying role.

Summary

1. The problem of the environmental control of the initiation of seasonal gonad development in birds was studied experimentally by giving attention to the factors of temperature and day-length at levels near those occurring in nature at the time of normal recrudescence.

2. Forty-seven male Juncos, collected at Chapel Hill, N. C., in January and February, were placed, in groups of seven to nine, on a 10-hr. photoperiod in warm cages from mid-February to mid-April. They were then placed for six weeks on photoperiods of either 12 hours or 11 hours, and in one case continued at 10 hours. One of the 12-hr. groups and one of the 11-hr. groups were transferred to a cold-room at 4°–8° C. for this period. Another 12-hr. group was placed in the cold-room for the dark period only, removed during the daily light period. One 12-hr. group, one 11-hr. group and the 10-hr. group were continued in the warm cages, where temperatures ranged from 24° to 29° C.

3. After six weeks, testes of birds in the 12-hr. warm group were about four times as large as testes of birds in either of the 12-hr. cold groups. Testes of birds in the 11-hr. warm group were nearly as large as those in the 12-hr. cold groups and were larger than those in the 11-hr. cold group. Testes of birds in the 11-hr. cold group were significantly larger than those in the 10-hr. warm group.

4. Thirteen of twenty-three birds on a 12-hr. photoperiod (56%) developed spermatozoa; one of seventeen on an 11-hr. photoperiod (6%) and none of seven on a 10-hr. photoperiod (zero %) did so.

5. Four additional males, in warm (20°–29° C.) cages with two females, were exposed to an 11-hr. photoperiod beginning at the winter solstice; after five months only one had developed spermatozoa. Range of testes development in this group was comparable to that in the 11-hr. warm group above.

6. In another experiment fifteen males were placed on an 11-hr. photoperiod beginning at the winter solstice; after six weeks none had reached spermatogenic stage IV. However, in the 10-hr. group above, one reached stage IV, one stage V.

7. From these data, and from consideration of the pertinent literature, it is concluded *a*) that low temperatures retard the rate of testicular recrudescence in Juncos, higher temperatures accelerating this rate; but *b*) that day-length is in some way an integral part of the mechanism of recrudescence, being either permissive or prohibitive of sperm development above or below approximately 11 hours,

temperature having here only a modifying role; and *c*) that although the existence of a critical, minimum length of day is not conclusively demonstrated, it is not contra-indicated, at least as regards the critical stages of completion of maturation divisions.

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